Notes from the Greenhouse World:
A Study in Coevolution, Planetary Sustainability, and Community Structure

Lee Worden[*,a]

[a]*Environmental Science, Policy and Management, University of California, Berkeley, CA 94720-3114 USA*

Abstract

This paper explores coevolution and governance of common goods using models of coevolving biospheres, in which adapting populations must collectively regulate their planet's climate or face extinction. The results support the Gaia hypothesis against challenges based on the tragedy of the commons: model creatures are often able to work together to maintain the common good (a suitable climate) without being undermined by "free riders." A long-term dynamics appears in which communities that cannot sustain Gaian cooperation give way to communities that can. This result provides an argument why a Gaia scenario should generally be observed, rather than a tragedy of the commons scenario. Second, a close look at how communities fail reveals failures that do not fit the tragedy of the commons framework and are better described in terms of conflict between differently positioned parties, with power over different aspects of the system. In the context of Norgaard's work, all these observations can be read as narratives of coevolution relevant to social communities as well as ecological ones, contrasting with pessimistic scenarios about common governance and supporting respect for traditional arrangements and restraint in intervention.

Key words: Gaia hypothesis, coevolution, sequential selection, adaptive dynamics, network dynamics, cooperation, tragedy of the commons, whole systems

1. Introduction

James Lovelock and Lynn Margulis's Gaia hypothesis was aggressively attacked almost immediately when it appeared in the 1970s. The hypothesis took a variety of forms ranging from "atmospheric homeostasis for and by the biosphere" (Lovelock and Margulis, 1974) to "She [the earth] is now through us awake and aware of herself" (Lovelock, 1979), and opponents tended to two lines of attack. One was to dismiss Gaia talk as "pseudoscientific mythmaking" (Postgate, 1988) because of poetic descriptions of the planet as a living organism or a conscious, deity-like being.

The other was by means of the newly emerging sociobiological vocabulary of "self-interest" and the "common good." In the same period of time, evolutionary biologists such as Richard Dawkins, E. O. Wilson, R. L. Trivers, and G. C. Williams had launched a comprehensive attack on the idea of the common good in evolution, exposing scenarios in which selection on members of a collectivity acts against the well-being of the collectivity those individuals belong to. These scientists successfully made the case that it is not sufficient to explain or predict an evolved feature that serves a group of organisms, or even a single organism, without explaining how selection acting on the smaller parts — organisms or their genes — does not destroy that feature.

Central narratives of this project, in addition to Dawkins's "selfish gene" (Dawkins, 1976), are the prisoner's dilemma of game theory (Rapoport and Chammah, 1965), Garrett Hardin's tragedy of the commons (Hardin, 1968), and the "problem of collective action," made formal by Mancur Olson (Olson, 1965) and others. These models come originally from political science and economics, and language is shared freely between evolution, politics and economics when they are used. Through this "contact language" (Turner, 2006), arguments about these issues in biology tend to be indirectly about what is possible in the social sphere as well.

The evolutionary attack on the Gaia hypothesis, introduced by W. Ford Doolittle (1981) and taken up by Dawkins (1982) and others, has come to be known as the "problem of the population of one" (Barlow and Volk, 1992). The problem is that for the different species of the earth to collectively regulate the atmosphere would be a kind of cooperation, or common good, and so it must be explained why species' "evolutionary self-interest" does not lead them to "free ride" and "enjoy the benefits" of a well-regulated climate without contributing to it. While this argument is closely related to Dawkins's discussion of "selfish genes," it is best understood as a version of the tragedy of the commons narrative structure, a connection which Dawkins makes explicitly. Populations of organisms stand in for animal herders, the climate takes the place of the common pasture, and the "temptation" to accept the

*Corresponding author

Email address: wonder@riseup.net (Lee Worden)

benefits of the common good without contributing is predicted to lead to collapse. This is called the "population of one" problem in this context because while organisms are given protection from destructive "selfish genes" by natural selection that weeds out unhealthy organisms, natural selection cannot operate on the whole biosphere because the biosphere does not reproduce and is not part of a population of similar entities, leaving the problem of how the biosphere could be protected from selfishness.

Attacks on the poetic-mythical language of Gaia advocates have subsided, as key figures including Lovelock and Margulis have affirmed their loyalty to science and cast their claims in the scientific language of biogeochemistry and mathematical models. The "population of one" issue is still alive, and Lovelock has even conceded the point (Kerr, 1988).

Lovelock, with Andrew Watson, introduced the Daisyworld family of models to demonstrate that a planetary ecological community can act as a global control system, keeping the climate within an optimal range for living creatures (Watson and Lovelock, 1983). The impressive range of Daisyworld models now in print does not resolve the "population of one" question, because some Daisyworld communities lose their ability to stabilize the climate when coevolution among the daisies modifies their relationship to the climate, though others do not (Wood et al., 2008).

In this paper I will present a series of models that provide evidence for "sequential selection," a phenomenon that can produce planetary ecological communities that stabilize themselves and the climate on both ecological and evolutionary timescales. Sequential selection is a direct response to Doolittle and Dawkins' tragedy-of-the-commons-based challenges to the Gaia hypothesis.

A few recent modeling efforts (Downing and Zvirinsky, 1999; Williams and Lenton, 2007) have demonstrated model communities that maintain environmental control on both ecological and evolutionary timescales. Williams and Lenton's simulated biospheres achieve regulation via high-level selection acting on an array of spatially distinct communities, a different mechanism from the one seen here, and Downing and Zvirinsky's models, while they demonstrate stable biospherical regulation without high-level selection and are rich in fascinating behavior, are complex and hard to analyze in detail, and the authors do not develop the arguments that I present here.

In this paper I present results from a model framework that is designed to have the richness of Downing and Zvirinsky's models, together with as much as possible of the simplicity and mathematical tractability of the Daisyworld models. These models do not allow selection among communities smaller than the whole biosphere. Additionally, unlike previous models, in this framework the desired climate is not specified by the modeler but negotiated by the model organisms collectively. These models explore when and how idealized global ecological communities can achieve collective atmospheric regulation. Model simulation results indicate that the tragedy of the commons scenario can happen, but suggest it is much less of a danger than attacks on Gaia seem to imply. Simple, uncontrived examples arise in which such a tragedy is not an issue, and it becomes clear how a global-scale self-organization process can produce a sequence of persistent, self-regulating biospherical communities.

2. Model Description

In the models I present here — the "Greenhouse World" family of models — the atmosphere is represented by a network of gaseous compounds and processes that transform various compounds into each other. Transformations happen both spontaneously, by simple chemical reactions, and as a byproduct of biological activity, like the transformation of CO_2 into O_2 by plants and other photosynthesizers. Global temperature rises and falls depending on the makeup of the atmosphere, and changing temperature helps or hurts the creatures in the system. Each population has an optimal temperature: it can only survive temperatures within a few degrees of its optimum, and produces offspring faster the closer the temperature is to its optimum. Simultaneously, the rise and fall of those populations' reproductive rates changes the atmospheric balance, which feeds back into the temperature. Equilibrium requires whole-system coordination of all these variables. These models are not intended to reflect actual climate dynamics realistically, only to provide a somewhat tractable testbed for propositions about what is possible in ecological communities.

Model equations are included in appendix A.1. The technical details of these models are dealt with in detail elsewhere (Worden and Levin, in preparation). Here I will present as few equations as possible, and present an overview of conclusions from the model experiments, explore further how exactly communities change, and discuss the results in relation to coevolution and how global-scale, sustainable ecological self-governance emerges and is maintained.

On a slower timescale than the above ecological process, the model species coevolve, responding together to their chemical and climatic environment at the same time as they co-create it. This is modeled by a technique known by its proponents as adaptive dynamics (Metz et al., 1996): when the ecological dynamics are at rest, introduce a single mutation — a small variant population identical to one of the established populations, except with a small, random positive or negative number added to its optimal temperature — and continue the ecological dynamics. Some variants thrive and old populations decline to extinction, and long-term changes in the community emerge. (In this model context, I use the term 'species' somewhat arbitrarily for a lineage of populations, which is subject to gradual evolutionary change as these variant populations arise and replace their predecessors, and 'community' for the collection of coexisting species at a given time.) In this model, variation is limited to these species' optimal temperature,
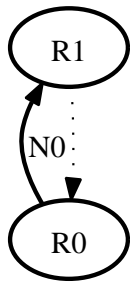
Figure 1: Material flows in a simple model ecological community. The one population, N0, consumes resource R0 and produces R1 as a waste product (solid arrow). R1 degrades chemically to R0 (dotted arrow).
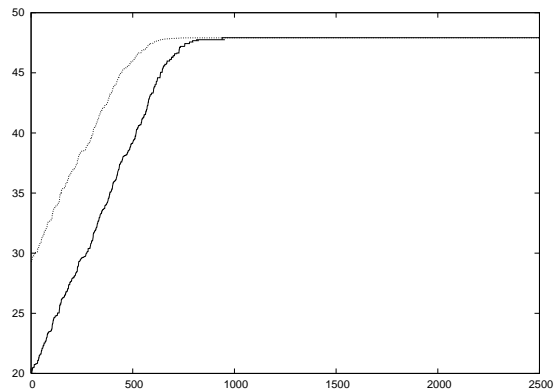

Figure 2: Evolution of optimal temperature in the model of figure 1. Time is on the horizontal axis, measured in number of mutations. Upper (dotted) line is global equilibrium temperature, lower (solid) line is optimal temperature of population 0.

allowing them to adapt incrementally to whatever temperature is currently found in the atmosphere.

This process of continuous coevolutionary change eventually comes to rest, and in extra-long-term experiments in qualitative change in community structure, a new species is added to the network at this point, with randomly assigned input and output resources and optimal temperature, and the ecological and evolutionary process continues from there. As we will see, these simulation experiments yield a significant conclusion — the emergence of stably self-regulating communities by means of sequential selection — that directly addresses the "population of one" question.

3. The simplest community

Figure 1 offers a very simple example of a model community structure. One species (labeled N0) consumes a gaseous resource, R0 (its "source resource"), and produces a different one, R1, as waste. Resource R1 spontaneously decomposes to R0, making a sustainable cycle possible. I assume R1 to be a greenhouse gas, such that if the entire ecosystem were made of R1 the temperature would rise to 100, and R0 to be a non-greenhouse gas, such that if everything were R0 the temperature would drop to 0. The shifting balance between R0 and R1 places the temperature somewhere between these two extremes.

The development of this model community in evolutionary time is plotted in figure 2. The species' optimal temperature is initially 20, and it can survive temperatures within 10 degrees of its optimum. This initial system comes to an equilibrium in which the atmosphere's temperature is nearly 30, which is not optimal for the species, but is survivable. As the species evolves, its optimal temperature shifts upward, toward the actual temperature, but each change in the species' population dynamics leads to a shift in equilibrium such that the equilibrium temperature also rises. The difference between optimal and actual temperature stays just under 10 degrees for a long time, but continually declines, and ultimately the two temperatures meet at about 48 degrees. When species N0's optimal temperature coincides with the actual global temperature,

its evolution stops, and the system does not change any further.

3.1. Evolutionary dynamics in the simple case: no tragedy of the commons

Now let us interpret the behavior of this model, first of all at the beginning of its history. This population requires a temperature between 10 and 30, and temperature is determined by the atmospheric balance that this population creates. These organisms cannot conspire (except in the etymological sense, meaning "breathe together"); they just dumbly produce offspring as quickly as the temperature allows them to. Without life, this planet's temperature would drop to 0. The N0 creatures raise the temperature above 0 by exhaling a greenhouse gas, R1. As temperature rises above 20 and their reproduction slows, we can imagine that that slowing could either speed up the rise in temperature further (a positive feedback) or suppress it (a negative feedback). Evidently it has a suppressing effect, or the temperature would rise beyond 30 and kill the N0 population. Similarly when temperature drops toward 20, the population's response does not drive it further down, which would be a destructive positive feedback. Instead it raises the temperature, stabilizing it at a survivable level. In this sense self-regulation prevails, and the birth rate and temperature come to balance each other. Should we view this as a counterexample to the tragedy of the commons scenario, which predicts that global self-regulated harmony should fail?

That would be premature, because that prediction should be taken in terms of evolutionary rather than ecological dynamics. That is, given a well-regulated biosphere, what is to prevent an antisocial population from arising, which takes advantage of the good conditions but does not help maintain them, making conditions worse for all parties? In this model, that would appear in the form of a variant population that flourishes in the climate it finds, and
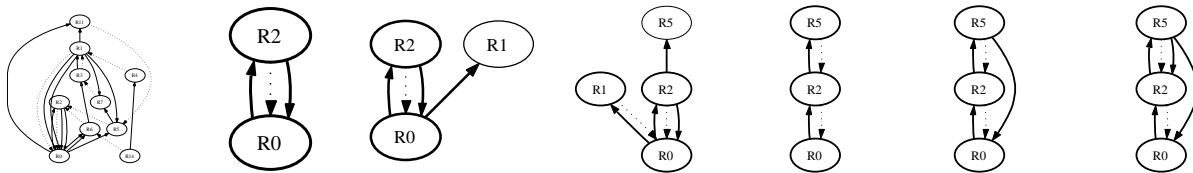
3

Figure 3: Community structure changing as ecological need arises. The first network pictured is randomly generated, and quickly collapses to the second structure shown. Two new species are added in succession, the second of which brings about two extinctions. Further additions and collapses follow, and the community repeatedly regains climate equilibrium when it is lost.

as it grows in number, either destabilizes the climate altogether, or leaves the climate worse for all surviving organisms than it was beforehand. The difference between a species's optimal temperature and the actual temperature is a convenient measure of species well-being in this model framework. Reproductive rate (i.e. fitness) is directly determined by that difference. Thus if a variant were either to drive itself and the older type to extinction, or to increase the gap between optimal and actual temperature — which would lead to "evolutionary suicide" if repeated enough — I would consider that an example of a tragedy of the commons.

In this model, to the contrary, the temperature gap declines at every step, until it reaches zero. By the above logic, this is a counterexample to the tragedy of the commons scenario. It follows that, at least in this model setting, the tragedy of the commons and its related scenarios involving selfishness, free riders, and defectors do not have predictive power. "Selfishness" does not necessarily undermine the sustainability of a common good.

In economics language, these tragic scenarios result from a perverse incentive structure, which places the participants' short and long term interests at odds with each other. Incentive structures that emerge in a given situation may or may not be perverse. In each case it is necessary to investigate whether perversity arises, and what determines whether or when it arises.

4. Complex communities: how sequential selection, driven by coevolution, can remove perverse incentives

A randomly generated community of atmospheric compounds and species that transform them is generally not viable as created. Such an assemblage tends to go through a period of climatic fluctuation and one or more extinctions. But an extinction changes the community to a different, simpler, assemblage, that embodies a different circuit of feedbacks. That configuration may or may not be viable or stable, and if not it will collapse to another community structure, which may or may not do better. In this way, the community will find its way to a stable form by repeatedly revising itself, if it can find such an arrangement before going to complete extinction.

In simulation experiments on such random communities, this search for an ecologically stable subcommunity is usually successful, for a broad range of choices of numerical parameters. When such a community is found, the process of coevolution may lead to further extinctions, or the community may come to evolutionary stability without loss. The resulting community, if total extinction is averted, is stable on two different time scales, both ecological and evolutionary.

Introduction of a qualitatively different species to an evolutionary stable community may or may not disrupt the community, and if it does, the above process of revision and re-stabilization repeats. Figure 3 presents the beginning of a sequence of community structures generated by this cycle. This simulated community came to evolutionary stability 17 times, passing through more than 25 network structures, before coming to total extinction.

4.1. Sequential selection weeds out dysfunctional communities

This process in which inviable community structures give way to viable ones by a sequence of restructuring events has been labeled "sequential selection" (Lenton, 2004; Lenton et al., 2004; Betts and Lenton, 2007), by analogy to the way natural selection removes poorly functioning organisms and cultivates those that are able to stay alive and reproduce. Like Darwinian selection processes, sequential selection can produce systems (communities, rather than organisms, in this case) that are not sabotaged by the "self-interest" of the parts that make them up. These ecological communities are stabilized by feedback processes in which global atmospheric temperature is an essential component, making the dynamic stability they exhibit inseparable from regulation of the climate.

Thus, in the process of sequential selection, these communities discard configurations in which climate regulation is undermined by any of the species present, or otherwise ineffective, and organize themselves into configurations where all species present contribute to climate control, or least do not sabotage it. In other words, sequential selection can get rid of communities with conflictual incentive structures, at least those that are bad enough to destabilize the community, and select communities with generally harmonious incentive structures. This offers an answer to the "population of one" question of why the biosphere should not be undermined by bad actors. Sequential selection is very different from Darwinian natural selection or other kinds of selection studied by evolutionists (to be discussed more below), but like those processes,

it can counteract selection on smaller scales, producing a larger-scale structure that is protected against "selfishness" of its components.

5. Coevolutionary dynamics in complex communities: cooperation, betrayal, and power

These models tell a story of a sequence of stable communities, punctuated by crises that flicker past as self-regulation is lost and re-established. Is it correct to describe this as periods of cooperation, separated by temporary attacks of tragedy of the commons? Let us look in some detail at how these communities fail.

First is an example where a new species is introduced and an old one disappears. The first three images in figure 4 show these changes in community network structure.

When the new species enters this community, consuming R7 and producing R1, resource R7 becomes far less available than before. This reduces the flow to the two resources and two species supplied by the decay of R7. The first of these two 'downstream' species declines to a very small population, and there is not enough left downstream of it to sustain the second species in line, which goes extinct.

In dynamics terms, one would say that the old community's equilibrium is made unstable by the introduction of the new variant, so that the dynamics leaves that equilibrium point, finding its way to a different stable attractor at which one of the old populations is reduced to zero. In ecological terms one might simply say that the new, invading species displaces a resident species. It is hard to see this as a tragedy of the commons: is the new species more selfish than the old one? The new community is very similar to the old one, and both stabilize at about the same temperature. An essential aspect of the tragedy of the commons is that the selfish party suffers along with everyone else, which does not happen here. We could say the new species killed the old one, invoking images of warfare or crime, but Hardin's narrative is a bad fit.

Later in this community's development, it acts out another scenario, which we might call "evolutionary murder," since one species is killed by the evolutionary development of the others. In this case, the second of the two species downstream of R7 is also killed as a result of the same invader, but this extinction happens well after the introduction, as a result of coevolution of the species together, not as a direct result of the introduction. This unfortunate species, like the one choking it off, needs to maintain its source resource at a particular level in order to survive. As the invader species evolves, becoming better adapted to the climate, it uses its source resource more efficiently and leaves even less of it in the air, reducing the flow to the downstream species and eventually making it unable to maintain enough source resource to survive. (For the mathematically inclined reader, because flows must balance at equilibrium, the R^* value for the upstream species equals the downstream species's R^* plus the downstream species's population size [see appendices A.2 and A.3], so that when the two R^*s become equal the population vanishes.)

This extinction happens gradually, the dying species' population becoming smaller with each evolutionary step of the upstream population, and finally vanishing, while the overall community never loses its dynamic stability or undergoes any discontinuous change.

The final collapse of this model planet's community results from a catastrophic loss of biospherical self-regulation. An invading species takes over the R1 niche from a predecessor, displacing it and another species that is fed by it (the two connecting R1 and R7). The gradual replacement of those two species by the new one brings with it a drop in temperature, very slow and slight at first, but then accelerating as the cooling hurts the remaining three populations and causes them to release more of their source resources and produce less of their products, which shifts the world much more drastically into a cooler regime. This is a runaway positive feedback that can not be corrected as extinctions cascade.[1]

This event does fit the tragedy of the commons mold. The invading species is responsive only to its own drive to reproduce, which has the side effect of destroying the environmental conditions it and all other life require for survival. In simulations I have run, this tends to happen after roughly 10 to 30 changes in community structure. From earlier discussion about distinguishing between perverse and cooperative incentive structures, one might think that each would arise about half of the time, but that result indicates that perverse structures, in the sense of those that destroy the community, are much rarer than that. Since each species here can only survive temperatures within 10 degrees of its optimum, and temperatures range from 0 to 100, this can be taken as evidence for a tendency for these communities to survive by negotiating a stably harmonious order, beyond random luck.

Also, it seems likely (though the complexity of the simulations has so far precluded collecting sufficient data to test this hypothesis directly) that as a community develops through addition and subtraction of species, it has the potential to become immune to further invasion. When a community is fully evolutionarily stabilized, a new species can only invade where there is a resource with no consumer. An evolutionarily stable community with an occupant in every niche would be permanently safe from disruption.

---

[1]For those who may be inspecting these model results in detail: this particular collapse seems to be a consequence of slight details. It actually would not have happened if the separation of timescales were modeled perfectly, because in that case all the existing species would be perfectly adapted to the climate, and the invader would not be able to displace its competitor. Instead, the existing consumer of R1 is almost perfectly adapted to the current climate, and the invader is just slightly better adapted. However, other simulation realizations produce collapses that don't rely on tiny imperfections, since a newcomer can enter that uses an unused resource: there would still be collapses if this kind of imprecision were removed.
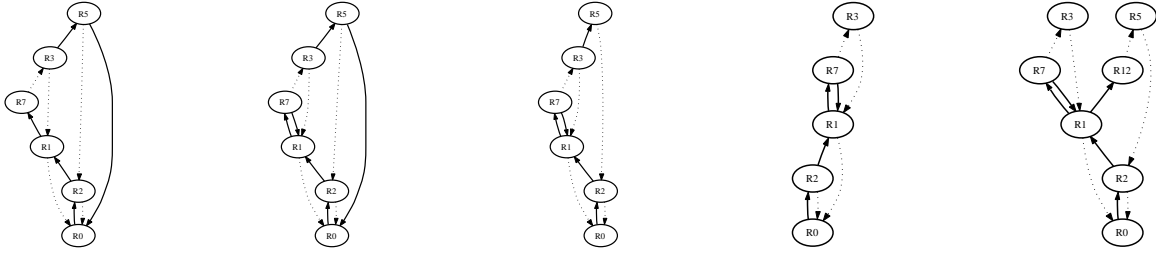
Figure 4: Species introduction and subsequent changes in community structure.

5.1. Ecological structural power

In the "murder" scenarios above, the only difference between the murderer and its victims is their position in the ecological network. Network structure facilitates this kind of "action at a distance," and also creates "keystone species" like the primary producer — the species that metabolizes resource R0, without which nothing else can survive because everything eventually decays to R0.

These situations are reminiscent of sociologists' "structural power," in which certain players in a community have the ability to determine outcomes and induce others to act in certain ways, by virtue of their placement in a social network. For example, if one is in the only position bridging two disjoint subnetworks, one can become a "broker" who has a monopoly on information each group wants about the other, or be especially creative by synthesizing ideas from the two sides (this is a structural hole, as in Burt, 1992). Individuals who are well-connected "network hubs" may have disproportionate influence over others. The special positions found in these Greenhouse World ecological networks are different from those standard cases, and there may be an opportunity for fruitful exploration of these kinds of structural effect in sociology or economics, as well as in ecology.

There is also an exceptional condition that can arise in these ecological models, which creates another kind of "ecological structural power." Every population in these models requires temperature within 10 degrees of its preferred temperature. When the climate fluctuates, survival depends on the presence of a feedback response to keep it within range. Thus the ability of a population to affect the temperature seems to be an important matter. Generally, all populations share control of the temperature, in the sense that temperature shifts when any of them changes slightly. However, there are exceptional communities in which equilibrium temperature depends only on two species out of a larger community. I have seen this happen in two ways. These are illustrated in figure 5.

In figure 5a, two species share a single source resource. This is generally not possible because of a rule of competitive exclusion that emerges from the ecological dynamics (see appendix A.2), but it can happen for a single pair of species, if the temperature can be steered to the one exact value that allows them to coexist, which is exactly halfway between those species' optimal temperatures.

In the community of figure 5b, a similar condition arises for different reasons. Here two species bring the temperature to a singular balancing point without sharing a source resource. This network is divided into two parts, connected only by the flows from the source resources of the two species in question. The flow from a species' source resource is directly related to the difference between its optimal temperature and the actual temperature (specifically, it is equal to that species' R^*, see appendices A.2 and A.3). Since these two flows must be equal at equilibrium, again, the equilibrium temperature must fall exactly between these two species' temperature optima.

As a result of this concentration of ecological control of the climate, as these communities develop coevolutionarily, the equilibrium temperature always falls exactly between the two controlling species' optimal temperatures. As those species evolve, the temperature changes accordingly, and other species must evolve fast enough to keep up, or they will die, since they cannot affect the temperature to keep it from going out of their range.[2]

These special power positions are also different from the sociologists' famous positions of structural power, and arise from global rather than local processes, since these interactions are mediated through the planetary temperature.

6. Sequential selection, multilevel selection, and social-cultural coevolution

Sequential selection is very different from the selection processes described by theorists of multilevel selection in evolution. For instance, group selection — survival of groups that survive and reproduce themselves better than others — can overpower individual selection in some cases when the two conflict, helping groups to develop means to keep defectors or free riders in check, or simply not have them (see, for instance, Boyd and Richerson, 2002). Similarly, individual selection can work against gene-level

---

[2]In practice this kind of extinction seems to be rare, since the two controlling species' optima, both evolving toward the actual temperatures, fall on either side of it, so the actual temperature tends not to change too drastically and other species are generally able to follow it successfully. Without further investigation, it is not clear whether these cases are particularly important to understanding which communities live or die.
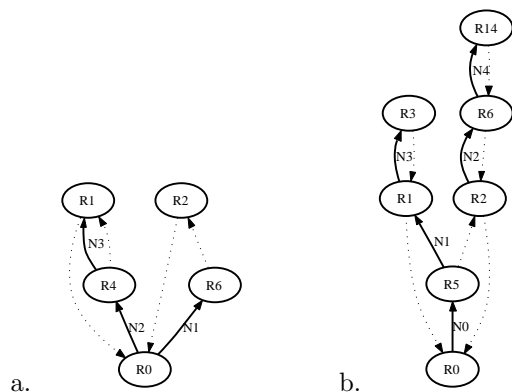
Figure 5: a. In this network, because species N1 and N2 share resource R0 by controlling the temperature, species N3 has no impact on the equilibrium temperature. b. In this network, because species N1 and N2 are associated with the resources flowing between otherwise disconnected network components, they determine the climate, and the other species have no impact on it.

selection, producing organisms that have means to keep "selfish genes" in check or that do not have such genes (e.g. Wilson and Wilson, 2007). While sequential selection similarly interacts with lower-level processes, producing planetary communities that are not undermined by "selfish" organisms, it is strictly speaking a theory of change and stabilization in an isolated system, whereas multilevel selection processes act in a population of similar, coexisting entities.

Strictly, then, if one were to try to apply multiple-level evolutionary or coevolutionary narratives to the subject how local or regional human communities change, such a discussion should probably draw on ecosystem selection (Swenson et al., 2000a,b) rather than sequential selection, because of contact and competition between different communities. Regardless, the two have much in common, and some of the conclusions of the present model may be of use in that discussion, and particularly in relation to Norgaard's image of a "coevolving cultural patchwork quilt."

In a patchwork of communities, we can consider communities coevolving with each other, and we can also consider each community being shaped by coevolution among its constituent parts. Sequential selection is an aspect of the latter coevolution process. It is emergent from the dynamics of coevolution within a community in the same way that Darwinian natural selection is emergent from ecological population dynamics.

A long-persisting social/cultural/ecological community pattern can be disrupted, or possibly even replaced, by individuals or social or cultural patterns arriving from somewhere else. Alternatively, disruption can come from gradual or abrupt change within the community. In either case, the community must from time to time either respond to perturbation, in accordance with its own internal processes, so as to preserve its patterns of organization, or change structurally. It is reasonable to think that a period of change may often be followed by arrival at a new pattern that has some level of stability and persistence, and that qualities that correlate with such persistent patterns are more likely to be observed at a given time than qualities that correlate with brief periods of change.

7. A Broader View of Ecological Governance

In these ecological models, sequential selection produces communities in which evolutionary incentives are aligned to stabilize coexistence, unlike the tragedy of the commons scenarios proposed by Doolittle and Dawkins. When those stable arrangements do collapse, the dynamics of the collapse also often do not fit the description of the tragedy of the commons.

The fact that the tragedy of the commons narrative structure does not accurately describe the events that shape these communities, which are often better described in terms of conflict, together with the possibility of an ecological analog of structural power, echoes ecologist Peter Taylor's critique of the tragedy of the commons in international politics (Taylor, 1998, 2005): "negotiations and contestations among groups with different interests, wealth and power—the messy stuff of most politics—are kept out of the picture. The 'tragedy' thus naturalizes the liberalized economics of structural adjustment and obscures the politics through which structural adjustment is imposed and implemented in poor, indebted countries" (Taylor, 1998). The "negotiations and contestations" by which the climate is collectively navigated by natural communities, when seen more clearly than the tragedy of the commons narrative allows, may help open a door to an understanding of "ecological politics" that not only clarifies our ecological theory but also helps to inform the crucial issues of how we may negotiate our own issues of sustainability and coexistence.

8. Conclusions

The Daisyworld models are presented as a "parable" demonstrating that Gaian regulation is a meaningful possibility (Watson and Lovelock, 1983). The Greenhouse World models, like the prisoner's dilemma and tragedy of the commons, can also be read as a parable. Here is one reading: common goods can in some cases be maintained without tragedy; communities can turn out to be undermined by selfishness far less often than pessimistic theories of altruism and defection would suggest; and when a disruption arises in a community, it can often be a matter of conflict between differently positioned actors rather than a tragedy of the commons. This underscores the general points that while it is valid to ask whether individual selfishness is a threat to any given common good, the answer may well be that it is not, and that beyond the question of how to overcome the problem of selfishness are the equally important questions of when it is a problem and when it isn't, and how to change the one case into the other.

These contentions are surely uncontroversial among many social scientists and others who work to expose the "messy stuff of politics" obscured by economistic narratives that deny differences in power and opportunity. Since evolutionary theory often naturalizes narratives about selfishness, altruism, free riding, and so on, and gives authority to proponents of individualistic, ahistorical social theories, perhaps these results can be of use to more institutionally or politically minded theorists, and in creating space for exploring scenarios of collective governance that are not supported by Hobbesian narratives of greed and competition.

This paper's theoretical results give support to the claims of Gaia theorists: that planetary homeostasis by and for the biosphere makes sense, and the planet can be expected to have some self-healing mechanisms. They also support some of the positions of skeptics, for instance that the planet's harmony isn't invincible and can be disrupted. They comport with a view of the planet that avoids extremes and is compatible with a contemporary understanding of climate science: there are global feedbacks that produce the climate we depend on, and they can be upset and give way to catastrophic runaway positive feedbacks. Both respect for the planet's long-standing, slowly constructed traditions of ecological governance and careful, responsible stewardship are called for.

The community structures predicted by sequential selection are not just an accidental mush of miscellaneous elements. They persist because they are able to maintain themselves, in other words because their overall structure is coherent, sustainable, and self-regulating. That coherence may have taken a very long time to develop. Disruptive interventions can lead to large-scale crisis and to collapse into an entirely different order. This argument is the same whether disruption comes from inside or outside the system. It is an argument for humility and respect for the wisdom of traditional practices and arrangements.

These models additionally offer an argument against the use of tragedy of the commons scenarios to justify "development" schemes such as structural adjustment (there are many such arguments, but why not add one more?). Group selection, kin selection, reciprocal altruism, social norms of reward or punishment, privatization or authoritarian control need not be invoked to dispel the specter of common tragedy. As in the curious little parables we have reviewed, a long-standing social/cultural/ecological community of organisms and practices can, by means of the self-organization process implicit in its history, have become organized so that its constituents do not encounter "temptation" that lures them to antisocial acts. Actually, disruption of an established order can introduce a destructive incentive structure, with the expected tragic consequences.

9. Acknowledgements

References

Barlow, C., Volk, T., Oct. 1992. Gaia and evolutionary biology. BioScience 42 (9), 686–693.

Betts, R., Lenton, T. M., 2007. Second chances for Lucky Gaia: a hypothesis of sequential selection. Gaia Circular, 4–6.
URL www.geolsoc.org.uk/webdav/site/GSL/shared/pdfs/\discretionary{-}{

Boyd, R., Richerson, P. J., 2002. Group beneficial norms can spread rapidly in a structured population. Journal of Theoretical Biology 215, 287–296.
URL http://www.sscnet.ucla.edu/anthro/faculty/boyd/\discretionary{-}{

Burt, R. S., 1992. Structural Holes: the structure of competition. Harvard University Press, Cambridge, MA.

Dawkins, R., 1976. The Selfish Gene. Oxford University Press.

Dawkins, R., 1982. The Extended Phenotype. Oxford University Press.

Doolittle, W. F., Spring 1981. Is nature really motherly? CoEvolution Quarterly Spring 1981, 58–63.

Downing, K., Zvirinsky, P., 1999. The simulated evolution of biochemical guilds: reconciling Gaia theory and natural selection. Artificial Life 5 (4), 291–318.

Hardin, G., 1968. The tragedy of the commons. Science 162, 1243–1248.

Kerr, R. A., 1988. No longer willful, Gaia becomes respectable. Science 38, 337–342.

Lenton, T. M., 2004. Clarifying Gaia: Regulation with or without natural selection. In: Schneider, S. H., Miller, J. R., Crist, E., Boston, P. J. (Eds.), Scientists Debate Gaia: The Next Century. MIT Press, Ch. 1, pp. 15–25.

Lenton, T. M., Caldeira, K. G., Szathmáry, E., 2004. What does history teach us about the major transitions and role of disturbances in the evolution of life and of the earth system? In: Schellnhuber, H. J., Crutzen, P. J., Clark, W. C., Claussen, M., Held, H. (Eds.), Earth System Analysis for Sustainability. Vol. 91 of Dahlem Workshop Report. MIT Press, pp. 29–52.

Lovelock, J. E., 1979. Gaia: A New Look at Life on Earth. Oxford University Press.

Lovelock, J. E., Margulis, L., 1974. Atmospheric homeostasis by and for the biosphere: The Gaia hypothesis. Tellus 26, 2–10.

Metz, J. A. J., Geritz, S. A. H., Meszéna, G., Jacobs, F. J. A., van Heerwaarden, J. S., 1996. Adaptive dynamics: a geometrical study of the consequences of nearly faithful reproduction. In: Strien, S. J. V., Lunel, S. M. V. (Eds.), Stochastic and Spatial Structures of Dynamical Systems. North Holland, Amsterdam, pp. 183–231.

Olson, Jr., M., 1965. The Logic of Collective Action. Harvard University Press, Cambridge, Mass.

Postgate, J., 7 Apr. 1988. Gaia gets too big for her boots. New Scientist, 60.

Rapoport, A., Chammah, A. M., 1965. Prisoner's Dilemma. University of Michigan Press, Ann Arbor.

Swenson, W., Arendt, J., Wilson, D. S., Oct. 2000a. Artificial selection of microbial ecosystems for 3-chloroaniline biodegradation. Environmental Microbiology 2 (5), 564–571.

Swenson, W., Wilson, D. S., Elias, R., Aug. 1, 2000b. Artificial ecosystem selection. Proceedings of the National Academy of Sciences of the USA 97 (16), 9110–9114.

Taylor, P., 1998. How does the commons become tragic? Simple models as complex socio-political constructions. Science as Culture 7 (4), 449–464.

Taylor, P. J., 2005. Unruly Complexity: Ecology, Interpretation, Engagement. University of Chicago Press.

Tilman, D., 1982. Resource Competition and Community Structure. No. 17 in Monographs in Population Biology. Princeton University Press.

Turner, F., 2006. From Counterculture to Cyberculture: Stewart Brand, the Whole Earth Network, and the Rise of Digital Utopianism. University of Chicago Press.

Watson, A. J., Lovelock, J. E., 1983. Biological homeostasis of the global environment: the parable of Daisyworld. Tellus 35B, 284–289.

Williams, H. T. P., Lenton, T. M., May 22, 2007. Artificial selection of simulated microbial ecosystems. Proceedings of the National Academy of Sciences of the USA 104 (21), 8918–8923.

Wilson, D. S., Wilson, E. O., Dec. 2007. Rethinking the theoretical foundation of sociobiology. The Quarterly Review of Biology 82 (4), 327–348.

Wood, A. J., Ackland, G. J., Dyke, J., Williams, H. T. P., Lenton, T. M., 2008. Daisyworld: A review. Reviews of Geophysics 46 (RG1001).

Appendices

A.1. Model equations

Population sizes are represented by N_i, for $i = 1$ to n_p; resources (atmospheric compounds) are R_j, for $j = 1$ to n_r; and global temperature is T. Each population has an optimal temperature τ_i. Intrinsic population growth rate, dependent on temperature, is

$$r_i(T) = R_{s(i)} u(T, \tau_i) = \begin{cases} R_{s(i)} r_0 \left(1 - \frac{(T - \tau_i)^2}{\sigma^2}\right) & \text{if positive} \\ 0 & \text{otherwise.} \end{cases}$$

Here $s(i)$ indexes the source resource of population i, meaning the one it consumes, $r_0 = 50$ is a rate constant for population growth, and $\sigma = 10$ is the maximum temperature deviation the population can tolerate. [In figure 3 σ is 16 rather than 10.]

Each resource is assigned a 'greenhouse constant,' or heating coefficient, H_j. Additionally, $p(i)$ indexes the resource produced by population i as waste, $\gamma = 1/2$ is the populations' efficiency of uptake of their source resources, $m = 1$ is the populations' mortality rate, $\rho = 1$ is rate of spontaneous chemical reduction, $red(j)$ is what resource j reduces to, $\Lambda = 1000$ is the rate of temperature change in response to the greenhouse effect, and M is the total mass of populations and resources (which is constant over time).

The model ecological dynamics are then

$$\begin{aligned} \frac{dN_i}{dt} &= \gamma \, r_i(T) \, N_i - m \, N_i \\ \frac{dR_j}{dt} &= \sum_{\{i|p(i)=j\}} (1 - \gamma) \, r_i(T) \, N_i \\ &\quad + \sum_{\{i|s(i)=j\}} (m - r_i(T)) \, N_i \\ &\quad + \sum_{\{j'|red(j')=j\}} \rho \, R_{j'} - \rho \, R_j \\ \frac{dT}{dt} &= \Lambda \left(\sum_j \frac{H_j \, R_j}{M} - T \right). \end{aligned}$$

A.2. The R^* result

Population sizes and resource concentrations at equilibrium, in general, are hard to analyze in this system without solving for all the system variables together. However, there is a simple result for the source resource of a population. Equilibrium conditions are found by equating the model dynamics equations (appendix A.1) to zero. In the case of the population dynamics equation, that gives

$$\gamma \, r_i(T) \, N_i - m \, N_i = 0,$$

which is solved either when $N_i = 0$, or when
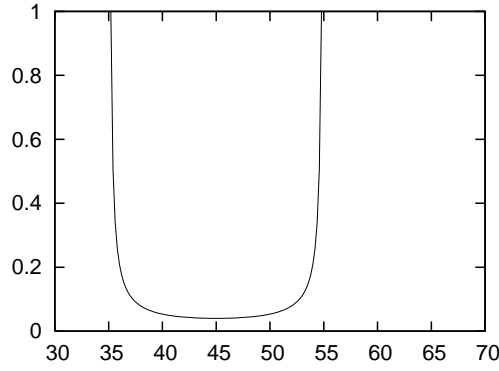
$$R_{s(i)} = \frac{m}{\gamma \, u(T, \tau_i)}.$$

9

Figure 6: $R^*(T, \tau)$ as a function of T, for a population whose optimal temperature τ is 45.
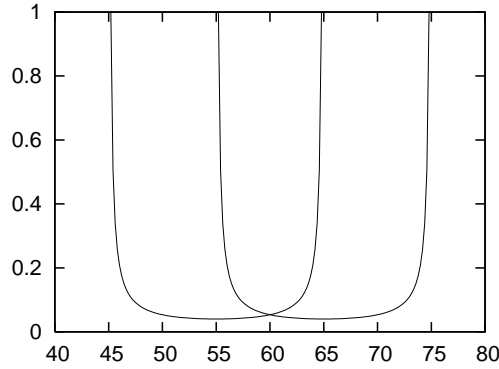

Figure 7: For two species with different τ, R^* is equal at only one temperature.

This means that for any population that is not extinct at equilibrium, its source resource must equilibrate at the above level, which we can call $R^*(T, \tau_i)$.

It follows that if two populations have the same source resource but different τ, since the source resource cannot equilibrate at two different levels, generally one of the two must go extinct. This result will be familiar to students of Tilman's work on resource competition in ecology (Tilman, 1982).

In this system, though, there is an exception to the standard R^* result, since R^* is a function of temperature, and population dynamics can change the temperature: if the temperature can be brought to exactly the value where two populations' R^* curves cross (figure 7), those two populations can coexist at equilibrium. This is a real possibility, as discussed in section 5.1. The crossing point is halfway between the two populations' optimal temperatures. For obvious reasons, when optimal temperatures are not specially chosen, this can only happen for one pair of populations out of the entire community at one time.

A.3. Balancing flows

If we examine the resource dynamics equations at equilibrium, as we did with the population dynamics equations to get the R^* result, we learn how to associate the population and resource variables with flows across the network. The R^* calculation tells us that at equilibrium $r_i(T) = m/\gamma$. Using that fact, the resource equation at equilibrium reduces to

$$0 = \sum_{\{i|p(i)=j\}} N_i \; - \sum_{\{i|s(i)=j\}} N_i \; + \sum_{\{j'|red(j')=j\}} R_{j'} \; - \; R_j.$$

The equilibrium flows across the arrows in a network are equal to the population size, for a (solid) arrow representing flow due to a population, or abundance of the decaying resource, for a (dotted) arrow representing decay of a resource. This is a balance equation, expressing that the total flow into a node of the network must equal the total flow out of it.